

Herbivore species and grazing intensity regulate community composition and an encroaching woody plant in semi-arid rangeland

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Grazing by livestock can influence ecosystems in various ways, including altering plant communities, influencing woody plant encroachment, and determining livestock productivity. Evaluating long term effects of grazing on plant composition is valuable not only to understand herbivory on rangelands, but to be able to address the primary factors that can threaten long term livestock productivity. We examined plant species composition and woody plant encroachment 45 years after the initiation of differing grazing treatments within a semiarid savanna of the southern Great Plains, USA. Grazing treatments varied in herbivore type (domestic cattle, sheep, and goats vs. goats only) and grazing intensity (heavy, moderate, and no-herbivory). All individual trees of *Juniperus ashei* Buchholz, the encroaching woody plant of the area, were removed prior to treatment initiation. Moderate and heavy grazing by a combination of species resulted in similar plant communities, while a history of heavy browsing by goats only and no-herbivory resulted in more distinct communities. Cover of *J. ashei* did not differ between mixed grazing and no-herbivory treatments, indicating that grazing was not responsible for woody plant encroachment. *Juniperus ashei* cover within the browsed treatment was a third less compared to other treatments; compositional differences within this treatment are possibly due to reduced cover of woody vegetation. Declines in livestock productivity of the area are likely related to compositional changes resulting from increased woody plants. Livestock production within this semi-arid rangeland is likely unsustainable without management of woody plant encroachment, as communities tend to a closed canopy woodland.

Keywords: cattle; Edwards Plateau; fire; grazing intensity; goats; herbivory; *Juniperus ashei*; livestock production

I. INTRODUCTION

While grazing can be important in shaping and maintaining grasslands and savannas (van Langevelde, et al., 2003), the type, intensity, and impact of herbivory can differ across ecosystems and management approaches (Milchunas, Sala, & Lauenroth, 1988). Grazing by domestic livestock for agricultural purposes can affect an ecosystem in many different ways, including altering plant community composition and diversity (Belsky, 1992; Augustine & McNaughton, 1998). Though often studied as a binary response (grazed vs. ungrazed), grazing effects are not exclusively regulated by simple defoliation, but influenced by many factors, including number of animals, species, and resource availability (Allred, Fuhlendorf, & Hamilton, 2011). For example, vegetation composition and diversity are influenced by differences in dental and digestive anatomy, as well as body size, among types and breeds of livestock (Rook, Dumont, Isselstein, Osoro, WallisDeVries, et al., 2004). In addition to changes in species composition, grazing can also alter the spatial heterogeneity of vegetation (Adler, Raff, & Lauenroth, 2001), which is critical for biodiversity and ecosystem function (Wiens, 1997). Selective or patch grazing by moose in boreal forest (Pastor, Dewey, Moen, Mladenoff, White, et al., 1998) and domestic livestock in tallgrass prairie (Fuhlendorf & Engle, 2004) resulted in greater spatial heterogeneity of vegetation.

In many grazing ecosystems around the world, the dominance of woody plants is increasing (Scholes & Archer, 1997).

These changes have consequences for plant composition, forage production, biodiversity, soil erosion, and hydrologic and carbon cycle impacts (Jackson, Banner, Jobbagy, Pockman, & Wall, 2002). Though grazing by domestic livestock is an often presumed mechanism of woody encroachment (Archer, 1994), variable grazing pressures, woody plant longevity, and lack of long term manipulations or observations make it difficult to evaluate the effect of livestock grazing on woody plant encroachment (Browning & Archer, 2011). Accounting for these factors will aid in understanding the effects of grazing on woody plant abundance.

Livestock production is a common and important economic practice on rangelands worldwide. Changes in plant communities and woody plant abundance can ultimately regulate livestock productivity (Burrows, Carter, Scanlan, & Anderson, 1990). Examining grazing effects on plant composition and, in turn, the consequences of these changes for livestock productivity, is necessary in evaluating the long term sustainability of livestock production. The Edwards Plateau, located within the southern Great Plains, USA, is well suited to assess the influence of grazing on vegetation dynamics in light of livestock productivity. Since the early 1900s, livestock production within areas of this region has steadily declined from 0.67 animal units (AU) ha⁻¹ in 1903 to 0.10 AU ha⁻¹ in 1997 due to reduced carrying capacity (Appendix A: Fig. 1; Smeins, Fuhlendorf, & Taylor, 1997; Walker, Johnson, & Taylor, 2005). Evaluating long term changes in vegetation resulting from grazing may identify mechanisms that contribute to the decline of livestock productivity.

In this paper we test the assumptions that grazing intensity and herbivore species alter plant community composition and determine the extent of woody plant encroachment. Our overall objective is to determine the long term effect of graz-

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ing on vegetation dynamics in the absence of fire. To do so, we analyze vegetation data collected in 1993, 45 years after the establishment of mixed species grazing treatments. We show that in the semiarid savannas of the Edwards Plateau, heavy and moderate mixed species grazing does not increase woody plant abundance and that the direct effects of grazing on plant composition are dependent upon herbivore species and grazing intensity, and are primarily through the regulation of woody plant encroachment.

II. METHODS

We conducted this study at the Texas A&M Sonora Research Station (30° 16' 0.1992" latitude, -100° 33' 55.1052" longitude), located within the Edwards Plateau of the southern Great Plains, USA. Annual precipitation averages approximately 600 mm; it is bimodal with largest amounts occurring in the spring and fall. Dominant herbaceous species include *Hilaria belangeri* (Steud.) Nash and *Bouteloua curtipendula* (Michx.) Torr. Dominant woody species include *Quercus fusiformis* Mill, *Q. pungens* Liebm var. *vaseyana*, and *Juniperus ashei*. Fires within the study area had not occurred for at least 100 years before data collection. Plant nomenclature follows Hatch, Gandhi, and Brown (1990).

A. Experimental design

In 1948, four grazing treatments were established that varied in grazing intensity and herbivore species. The heavily grazed treatment consisted of two 32 ha pastures, continuously stocked with a combination of cattle, sheep, and goats. Stocking rates within the heavily grazed treatment varied (Table 1), but from 1948 to 1983 were 30-40% greater than the moderately grazed treatment. The moderately grazed treatment consisted of two 24 ha pastures with a combination of cattle, sheep, and goats at a moderate stocking rate of 0.12 ha animal unit year (AUY) ha⁻¹; stocking rate was reduced to 0.09 AUY ha⁻¹ from 1987 to 1993. This treatment was part of a four pasture, three herd rotational grazing system. Heavy and moderately grazed treatments had a 2:1:1 (animal units) cattle, sheep, and goat ratio. The browsed treatment consisted of two 32 ha pastures that were browsed heavily and continuously by goats from 1948 to 1969 at a stocking rate of 0.18 AUY ha⁻¹. From 1970 to 1993 the browsed treatment was moderately and continuously grazed by a combination of cattle, sheep, and goats at stocking rates similar to the moderately grazed treatment. The cattle, sheep, and goat ratio changed from 3:1:1 to 2:1:1 (animal units) during this time. The no-herbivory treatment consisted of two 12 ha pastures that had not been grazed by livestock since 1948.

At the time of treatment establishment, all *Juniperus ashei* individuals were removed by hand from each pasture, and all pastures had similar plant composition (Smeins & Merrill, 1988; Smeins, et al. 1997). Though treatment replicates have been cited as having similar plant composition prior to the beginning of treatments, we recognize the lack of pre-treatment

data for specific analyses within this paper. For all pastures in the experiment, the grazing history before 1948 was heavy, continuous use. Treatments are summarized in Table 1.

B. Sampling design

We examined plant species composition of treatments in June and July of 1993, 45 years after treatment initiation. We established two sets of ten 50 m parallel lines in each treatment replicate. We estimated canopy cover of each species, as well as cover of litter and rock, every alternate meter along each line using a 0.10 m² quadrat and Daubenmire cover classes (Daubenmire 1959). Woody species greater than 1.5 m tall were recorded separately from those shorter than 1.5 m. Environmental data collected at each quadrat included average rock size (less than 5 cm, 5-15 cm, and greater than 15 cm in diameter), soil depth (less than 5 cm, 5-25 cm, and greater than 25 cm), and slope (0-2%, 2-3%, and 3-5%).

C. Analysis

To determine the effect of grazing on the cover of woody species *Juniperus ashei*, *Quercus fusiformis*, and *Q. pungens* (dominant woody plants), we averaged quadrats in each treatment unit and used individual analyses of variance to examine treatment differences in percent cover. We calculated species richness and Shannon's index of diversity for each treatment replicate. We also calculated the frequency of *Juniperus ashei* using quadrats within each treatment replicate. We used analysis of variance to examine richness, diversity, and *J. ashei* frequency differences among treatments.

We used Detrended Correspondence Analysis (DCA; Hill & Gauch, 1980) to examine the effects of grazing treatments on plant community composition. DCA is an ordination technique that can be used to summarize similarities and differences among plant communities and infer relationships between sites and environmental gradients (Digby & Kempton, 1987). Due to sampling design (quadrats within transects within pastures), we analyzed data at three spatial scales. We used the range of DCA site scores to assess spatial heterogeneity of vegetation at each particular scale (Fuhlendorf & Engle, 2004). Broad scales were measured at the pasture level; species abundances were averaged across all quadrats within a pasture. Intermediate scales were measured at the transect level; species abundances were averaged within transects in a pasture. Fine scales were measured at the quadrat level; species abundances of each individual quadrat were used.

We used Canonical Correspondence Analysis (CCA; ter Braak, 1986) to examine the influence of environmental variables on species composition within each grazing treatment. CCA is an ordination technique that can also be used to summarize similarities and differences among plant communities. CCA differs from DCA in that environmental gradients (explanatory variables) are known and measured, and are included in the ordination. Permutation tests can be used to test

Treatment	Livestock	Stocking rate (AUY ha ⁻¹)	Species Ratios (AU; cattle:sheep:goat)	Goat stocking rate (AUY ha ⁻¹)
Heavy				
1948-1969	cattle, sheep, goats	0.18	2:1:1	0.04
1970-1982	cattle, sheep, goats	0.20	2:1:1	0.05
1983-1986	cattle, sheep, goats	0.12	2:1:1	0.03
1987-1993	cattle, sheep, goats	0.09	2:1:1	0.02
Moderate				
1948-1986	cattle, sheep, goats	0.12	2:1:1	0.03
1987-1993	cattle, sheep, goats	0.09	2:1:1	0.02
Browse				
1948-1969	goats	0.18	n/a	0.18
1970-1986	cattle, sheep, goats	0.12	3:1:1	0.02
1987-1993	cattle, sheep, goats	0.09	2:1:1	0.02
No-herbivory	n/a	n/a	n/a	n/a

TABLE I: Summary of grazing treatments from 1948 to 1993 at the Texas A&M Sonora Research Station within the Edwards Plateau, southern Great Plains, USA. Though stocking rates were variable, from 1948 to 1982 grazing intensity in the heavily grazed treatment was 30-40% greater than the moderately grazed treatment. At the time of treatment establishment in 1948, all *Juniperus ashei* individuals were removed by hand from each pasture, and all pastures had similar plant composition. Animal unit year (AUY) = 4368 kg or the amount of forage consumed by one 455 kg animal for one year. Animal Unit (AU) = one 455 kg animal.

for significance of explanatory variables. To determine the influence of *Juniperus ashei* on plant communities, we removed *J. ashei* as a species and its percent cover was included as an explanatory variable in the CCA, along with litter, rock, soil depth, and slope. CCA was performed within each treatment separately using species abundances of each individual sample quadrat. A permutation of 1,000 iterations was used to test the significance of constrained eigenvalues of all CCAs. We performed all analyses in R (R Development Core Team, 2011), using the vegan package (Oksanen, Kindt, Legendre, OHara, Simpson, et al., 2011) for DCA and CCA.

III. RESULTS

Heavy browsing by goats reduced cover of the woody plant *Juniperus ashei* ($P < 0.05$), but not *Quercus fusiformis* or *Q. pungens* (Fig. 1). *Juniperus ashei* cover in the browse treatment was approximately one third compared to other treatments. Species richness was greatest in the no-herbivory treatment, and was nearly twice as much as in the heavily grazed treatment (Table 2). Diversity (Shannon's index) was similar across all treatments; though frequency of *J. ashei* appeared low in pastures heavily browsed by goats, frequencies did not differ among treatments (Table 2). *Hilaria belangeri*, a common grass species for the region, was present in all treatments, while *Eriochloa sericea* (Scheele) Munro ex Vasey, a highly palatable forage for livestock, was absent in the heavy grazing treatment. Rock and litter cover were also high in all grazing treatments (see Appendix A: Table 1 for relative abundances of all species).

DCA showed differences in plant community composition and spatial heterogeneity among grazing treatments (Fig. 2). At the broadest scale (pasture level), the ordering of sites along DCA axis 1 indicated a gradient based upon grazing treatment; sites with no herbivory were situated on the far right, while sites initially browsed by goats were on the far left. The first two axes of the DCA accounted for 82% of

Treatment	Richness	Diversity	<i>J. ashei</i> freq.
Heavy	45.5 (2.5) ^a	2.24 (0.06)	32.5 (12.3)
Moderate	69.5 (9.5) ^{ab}	2.42 (0.16)	26.2 (4.5)
Browse	70.0 (3.0) ^{ab}	2.47 (0.03)	9.9 (1.5)
No-herbivory	88.0 (13.0) ^b	2.50 (0.08)	32.2 (3.1)

TABLE II: Mean species richness, mean diversity (Shannon), and mean frequency of *Juniperus ashei* (calculated using quadrats within each treatment replicate) for grazing treatments (n=2). Number in parentheses represents one standard error. Different letters indicate differences among treatments (ANOVA and Tukeys HSD, $P < 0.05$).

the variance, with eigenvalues of 0.1654 and 0.0895, respectively. DCA site scores revealed distinct separation among treatments. The heavy, moderate, and no-herbivory treatments were more similar to one another, while browse treatments (heavy utilization by goats for approximately 20 years, moderate utilization by cattle, sheep, and goats thereafter) were more distinct. Spatial heterogeneity (measured by the range of DCA site scores) at the broad scale was greatest in the moderately grazed treatment and least in the heavily grazed treatment.

At intermediate scales (transect level), the range of DCA site scores overlapped considerably, indicating that plant composition was more similar among treatments at this scale. The first two axes of the DCA accounted for 63% of the variance, with eigenvalues of 0.3659 and 0.2974, respectively. Mean DCA site score of the browse treatment was more distinct than for the other treatments, but was well within the variation of other treatments. At the intermediate scale, spatial heterogeneity was greatest in areas with no herbivory. At fine scales (quadrat level), the range of DCA site scores for each treatment were similar to one another and overlapped. The first two axes of the DCA account for 56% of the variance, with eigenvalues of 0.8198 and 0.6968, respectively. Similar to the intermediate scale, mean DCA site score of the browse treatment was more distinct compared to other treatments.

The explanatory variables of CCA within each grazing

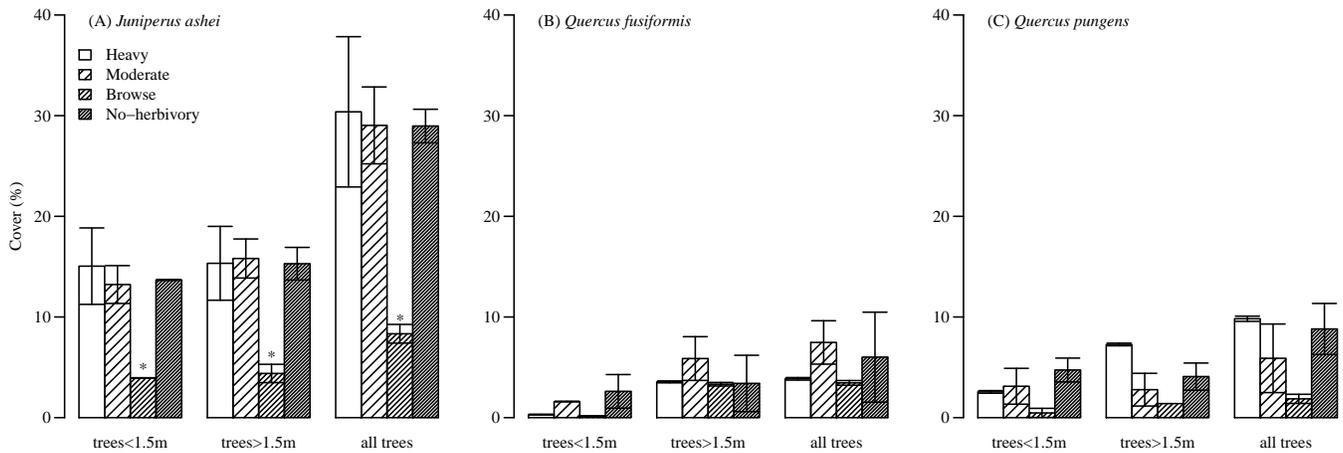


FIG. 1: Percent cover of dominant woody species (A) *Juniperus ashei*, (B) *Quercus fusiformis*, and (C) *Quercus pungens* after 45 years of grazing treatments. Prior to establishment of treatments, all *J. ashei* individuals were removed by hand. Cover was measured separately for trees less and greater than 1.5 m in height. ANOVA and Tukeys HSD were used to examine differences among all treatments within tree size classes (trees < 1.5 m, trees > 1.5 m, and all trees). Asterisk (*) indicates significant difference ($P < 0.05$) within species and tree size class. Bars are means (pastures; $n=2$), error bars are one standard error. Table 1 summarizes treatments.

treatment were significant ($P < 0.05$). The influence of *Juniperus ashei* cover on the plant community appeared strongest in the heavily grazed and no-herbivory treatments (Fig. 3). *Juniperus ashei* cover limited distribution of nearly all species, including the most common herbaceous plants. Litter and soil depth also had a strong influence in all treatments; the influence of rock size and slope were similar among treatments. Plant species within each treatment responded similarly to local environmental variables.

IV. DISCUSSION

Grazing by domestic livestock can influence plant community composition, but is not a simple binary effect (e.g., grazing vs. no grazing). In the semiarid grasslands of the southern Great Plains, plant composition was dependent upon herbivore species and grazing intensity. A combination of domestic cattle, sheep, and goats at heavy and moderate grazing intensities produced similar plant communities, while initial heavy utilization by goats generated a distinct community. The difference in composition from goat browsing is likely attributed to the initial heavy consumption of the woody plant *Juniperus ashei*, with continued moderate browsing thereafter. Percent cover of *J. ashei* within browsed treatments was three times less than other treatments. This browsing effect on woody establishment and cover has been shown in other ecosystems, specifically African savannas (Prins & van der Jeugd, 1993; Moe, Rutina, Hytteborn, & du Toit, 2009).

Heavy consumption of *Juniperus ashei* within the browse treatment is the potential mechanism of its reduced cover. Due to secondary compounds present in leaves, palatability of *J. ashei* is reduced and often protected from herbivory (Riddle, Taylor, Kothmann, & Huston, 1996). Though goat grazing with a combination of livestock can increase dietary range and consumption of less palatable plants (Utsumi, Cibils, Es-

tell, Baker, & Walker, 2010), suppression of *J. ashei* did not occur with mixed species grazing alone. The differences in stocking densities suggest that it is not simply the presence of goats, but the intensity of their browsing that is important for woody plant suppression and overall vegetation impact. Greater densities of goats result in greater dietary range (animals are forced to eat less palatable forage), create a higher goat to *J. ashei* ratio, increasing per goat consumption of *J. ashei* (Taylor, Launchbaugh, & Huston, 1997; Utsumi et al., 2010). Maintaining this high ratio of goat to *J. ashei* is likely necessary to prevent or reduce encroachment, and is evident from the browse treatment. *Juniperus ashei* cover was lowest within this treatment, where goat stocking rate was 78% and 84% higher than heavy and moderate treatments, respectively, from 1948 to 1969. The switch from heavy goat browsing to moderate mixed grazing in 1970 resulted in an approximate 90% decrease in goat stocking rate, reducing the goat to *J. ashei* ratio, and decreasing overall consumption of *J. ashei*. Although untestable without vegetation data prior to the lowering of stocking density and the switch in herbivores, the reduced goat to *J. ashei* ratio may have been sufficiently low to decrease herbivore pressure on *J. ashei* altogether, allowing cover to increase to levels present when sampled in 1993.

The indirect effects of grazing on plant composition appear to operate specifically through the manipulation of the woody species *Juniperus ashei*. The reduced amount of light near and underneath *J. ashei* trees will alter composition, particularly decreasing cover of graminoid species more than forbs (Fuhlendorf, Smeins, & Taylor, 1997). Leaf litter accumulation of *J. ashei* can further reduce light availability to germinating plants and influence soil processes, including nutrient cycling and decomposition (Yager & Smeins, 1999). The overreaching effect of *J. ashei* on composition is evident when comparing the browse treatment to other grazing treatments. Initial heavy use by goats only, followed by 25 years of moderate grazing by cattle, sheep, and goats, reduced *J. ashei* cover

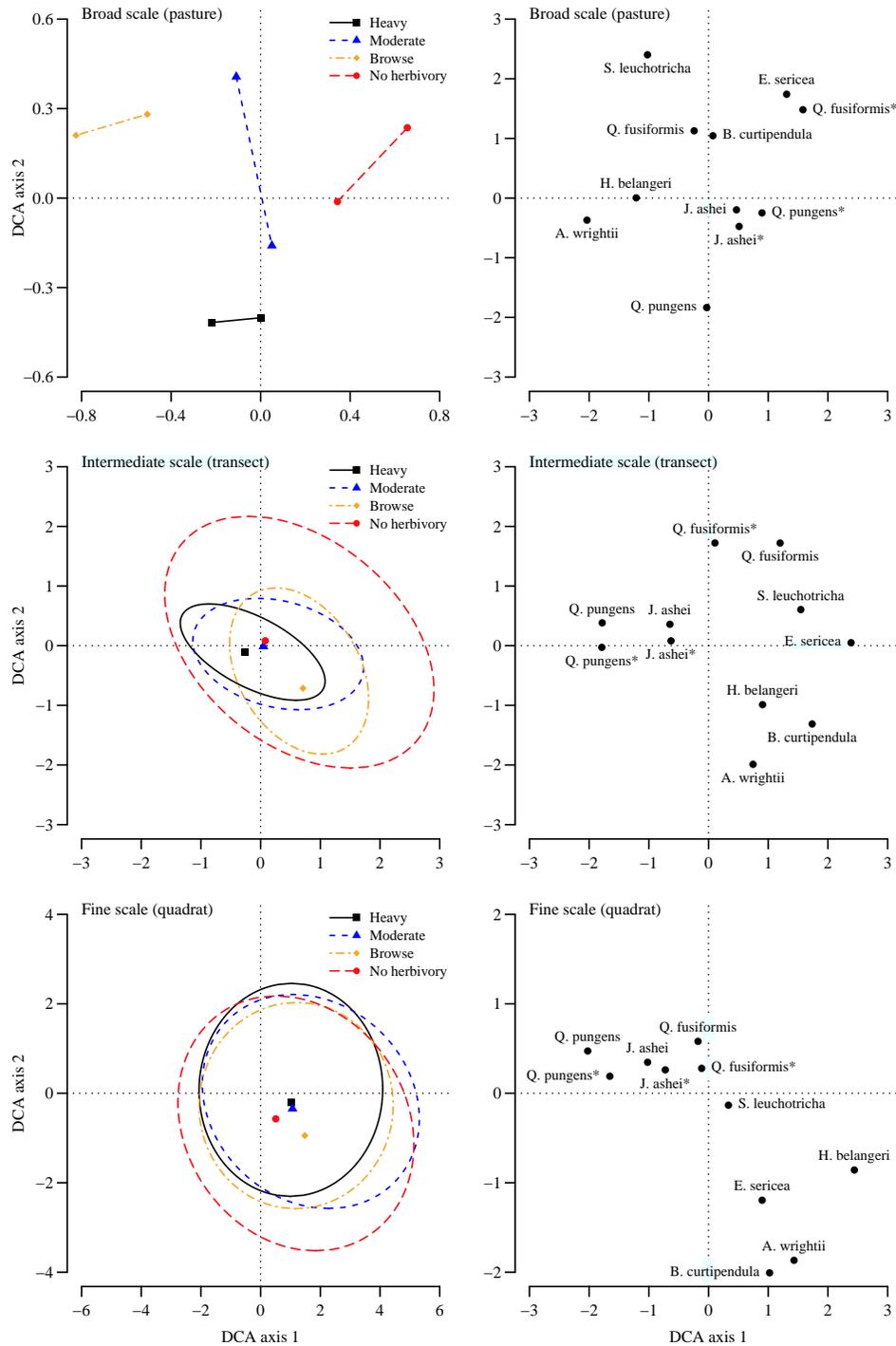


FIG. 2: Detrended correspondence analysis (DCA) of plant community after 45 years of grazing treatments, analyzed at three spatial scales. Left column shows site information for first two axes of DCA; data points are site scores (broad scale) or mean site scores (intermediate and fine scales). Line segments indicate distance between samples (broad scale) while ellipses encompass all samples within a treatment (intermediate and fine scales). At broad scales, the ordering of sites along DCA axis 1 indicated a gradient based upon grazing treatment; sites with no herbivory were situated on the far right, while sites initially browsed by goats were on the far left. Right column shows species scores for first two axes of DCA. Only the most common species are plotted (*Aristida wrightii*, *Bouteloua curtipendula*, *Eriochloa sericea*, *Hilaria belangeri*, *Stipa leuchotricha*, *Juniperus ashei*, *Quercus fusiformis*, *Q. pungens*). Asterisk (*) indicates woody species less than 1.5 m in height. Note scale differences among graphs. Table 1 summarizes treatments.

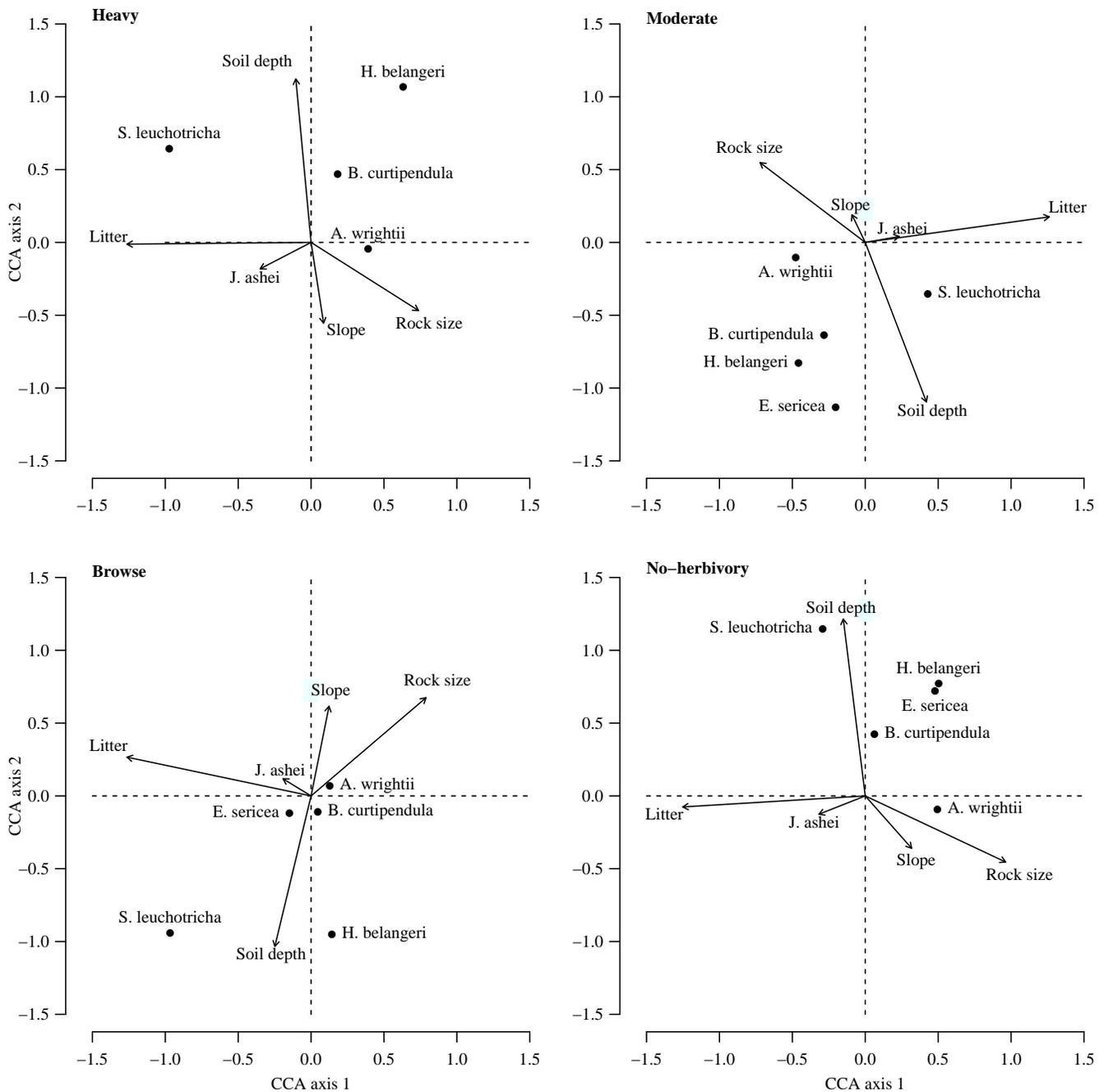


FIG. 3: Scores of environmental variables and species from canonical correspondence analysis (CCA) within each particular grazing treatment. Arrows represent environmental variables litter, rock size, soil depth, slope, and cover of *Juniperus ashei*; direction of arrow indicates gradient and length of arrow is proportional to the strength of correlation. Only the most common herbaceous species are plotted (*Aristida wrightii*, *Bouteloua curtipendula*, *Eriochloa sericea*, *Hilaria belangeri*, and *Stipa leuchotricha*). Nearly all species were negatively correlated to *J. ashei* cover, indicating the influence of this encroaching woody plant. Table 1 summarizes treatments.

and produced a distinct community compared to similar treatments with the same mix of animals. While CCA showed that the influence of *J. ashei* on community composition is similar among treatments, with little or no herbaceous species underneath canopies, the abundance of *J. ashei* in the browse treatment is much less and therefore creates a more distinct plant

community. In this ecosystem, the abundance of encroaching woody plants is likely just as important as grazing in determining plant composition.

While long term moderate or heavy grazing by the combination of animals did not affect the abundance of *Juniperus ashei* or overall community composition, other forms of

grazing or grazing management may produce different effects. Grazing followed by long recovery periods may stimulate grass production, reducing overall tree growth (Riginos, 2009), and grazing in conjunction with fire may also limit the rate of increase for invasive species (Cummings, Fuhlendorf, & Engle, 2007). In our study, heavy grazing also resulted in more homogeneous defoliation and consistently reduced heterogeneity at all scales examined. Decreased heterogeneity after herbivory is often a result of the lack of patch grazing (i.e., more homogeneous grazing), and is likely to reduce habitat and organism diversity at many levels (Adler et al., 2001).

The decreased carrying capacity of livestock at this site is the result of ecosystem changes. It is unlikely, however, that grazing is entirely responsible for the overall reduction of carrying capacity; if it were, decreases in stocking rates over the years would restore higher capacities or at least maintain capacities, which did not occur. Additionally, some of the changes we observed occurred equally in ungrazed treatments. Cover of *Juniperus ashei* increased approximately 30% (from 1948 when all trees were removed) across heavily, moderately, and ungrazed treatments. Heavy livestock grazing is often an assumed mechanism of woody plant encroachment, in which grazing reduces the competitive effect of grasses on tree saplings (Archer, 1994; Riginos, 2009). Our findings contradict this assumption, as heavy and moderate grazing did not increase tree cover compared to no grazing. Similar results have been found with shrubs and trees of other systems (Browning & Archer, 2011), indicating that other mechanisms may be primarily responsible for woody plant encroachment.

The cover and increase of woody plants within this region was historically controlled by fire (Fuhlendorf, Smeins, & Grant, 1996). Since European settlement, however, fire has been reduced or prevented altogether, while grazing by domestic livestock has increased. Without fire, increasing cover of *Juniperus ashei* may likely continue and create a closed canopy woodland that further alters species composition and livestock carrying capacity. Though heavy browsing by domestic goats, or use of mechanical or chemical methods, may mimic some of the defoliating effects of fire, specific responses between fire and grazing often differ (Limb, Fuhlendorf, Engle, & Kerby, 2011) or interact to provide greater effects (Staver, Bond, Stock, van Rensburg, & Waldram, 2009).

At this specific site, overall livestock productivity has declined while cover of the encroaching woody plant *Juniperus ashei* has increased. Goats may be an effective management tool to reduce or maintain grasslands heavily encroached by *J. ashei*. More research is needed to determine optimum stocking densities and to detect thresholds at which goats successfully regulate *J. ashei*. Moreover, as the cover of *J. ashei* appeared to be a dominant driver of plant community composition, the changes resulting from woody plant encroachment may be as significant as those from herbivory. In the semi-arid rangelands of the Edwards Plateau, management of woody plants, through herbivores, fire, or other means, may be just as critical as grazing management for sustainable livestock production.

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